THE DEVELOPMENT AND STRUCTURE OF THE TAIL IN WOODPECKERS

by

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INTRODUCTION

The purpose of this paper is to give as complete an account as possible of the development and function of the tail in woodpeckers, and then to compare the skeletal parts in the different species to note the morphological differences that occur. Attention is also called to the slight variations that appear in individuals of the same species.

Although there has been considerable work done on bird skeletons, practically nothing is to be found on the skeleton of the tail except of a very general nature. Dr. R.W. Shufeldt gives the only account the writer has been able to find that deals exclussively with the skeletons of woodpeckers (On the Osteology of Woodpeckers). Proc.Amer. Phil. Soc. Phil. Oct-Dec. 1900. vol. 39, No. 164). This work is far from complete and only mentions the tail bones in a small number of species. Other workers who have contributed to the knowledge of the bird skeleton are: F.A. Lucas, St. George Mivart, W.B. Pycraft and W.K. Parker. Further work along this line will probably bring out morphological differences to substantiate the present classification which is so often based on external characters alone. For the classification Robert Ridgway's "Birds of North and Middle America was followed.

MATERIAL AND ACKNOWLEDGMENTS

Material for histological study was obtained from the one species, *Colaptes auratus luteus*. Eggs were collected from the nests, the embryos removed and placed in fixing fluid. They were later imbedded in paraffin and sectioned. Unfortunately, stages sufficiently early to show the development of the feathers and bones from the beginning were not obtained in time to be included in this paper. It is hoped that the early development will be added later.

Fresh bodies of *Colaptes auratus luteus* were dissected for the study of the musculature of the tail.

Skeletal material was obtained from the following sources: Mr. C.D. Bunker, Assistant Curator in Charge of Birds and Mammals at the Kansas University Museum, placed at my command the skeleton collection of the Museum; twenty seven skeletons, including nineteen species, were obtained from the U.S. National Museum through the courtesy of Dr. Alexander Wetmore of the Smithsonian Institution; two specimens from the Museum of Vertebrate Zoology at Berkeley California through the kindness of Dr. Joseph Grinnell; and eleven specimens from Mr. James Moffitt of Tahoe City, Lake Tahoe Calif. To all the above gentlemen I wish to express my sincere thanks. I wish to further express my appreciation to Mr.C.D. Bunker for the many helpful suggestions and

the kind assistance he has given me from time to time; also to Dr. Alexander Wetmore for suggesting the problem. To Dr.H.H. Lane of the Zoology Department, under whose supervision I was working, I am greatly indebted for the kind assistance and many helpful suggestions and criticisms concerning my work.

EXPLANATION OF TERMS

Length of pygostyle- distance from the point of the neural spine to the base of the terminal disc, LPiin Table I.

Width of pygostyle- the greatest distance across the terminal disc, WP in Table I.

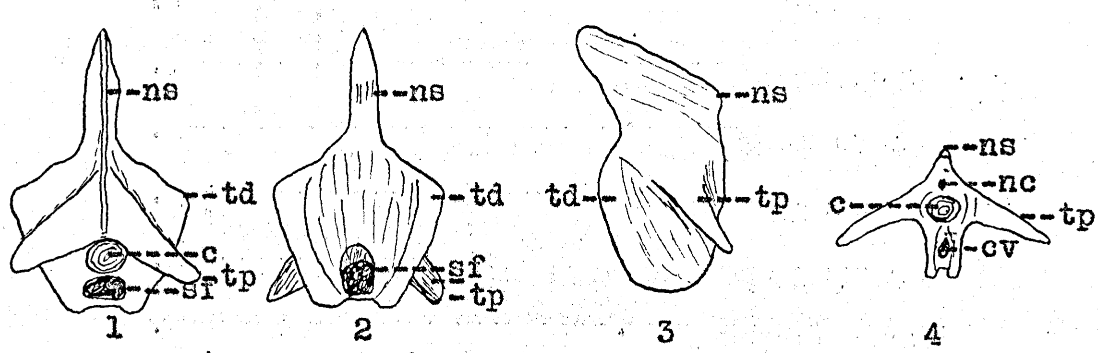
Projection of spine- The distance the neural spine extends from the top of the terminal disc as measured from the posterior surface, PS in Table I.

Width of transverse processes- the greatest distance from the tip of one process to the tip of the other, outside measurement, TrP in /Table I.

Length of skull- the greatest length of the skull, LS in Table I.

Percent pygostyle of skull is denoted by, %, in Table I.

The following drawings are of typical caudal vertebrae. Numbers 1,2 and 3 are anterior, posterior and lateral views respectively of the pygostyle. Number 4 is an anterior view of the free caudal joining the pygostyle.



c, centrum; cv, chevron bone; ns, neural spine; nc, neural canal; td, terminal disc; tp, transverse process; sf, submarginal foramen.

DEVELOPMENT

The ancient bird, Archaeopteryx , possessed a long lizard-like tail of twenty one vertebrae of which, each, from the ninth to the twentieth, supported a pair of well developed rectrices (Newton. A Dictionary of Birds) p 753). The vertebrae were in a long chain and not compressed as in modern birds. Such a tail doubtless had some use as a steering organ. In modern birds, the shortened, much compressed tail ends, as a rule, in a fused portion- the "rump post" or pygostyle. The ten strong and two rudimentary rectrices which are present in all woodpeckers, are inserted laterad to the large neural spine and anterior to the terminal disc so they are fan shaped in arrangement.

The early stages in the development of the bones in Colaptes auratus luteus show six segments in the pygostyle, Huxley gives ten segments in the pygostyle of the swan which is a more pmimitive bird than the woodpecker. In C. a. luteus five vertebrae anterior to the pygostyle remain free and six urosacrals fuse with the post-ilia. This gives us in all seventeen post-sacral vertebrae, only four less than was found in Archaeopteryx. It is evident then that the shortening of the tail is not due so much th the reduction in number of vertebrae, but to fusion and compression of the component parts .

The neural canal passes through the pygostyle and opens posteriorly until just before hatching when the foramen is closed in by a growth of bone; however the canal penetrates the pygostyle for some distance in the adult bird.

Fusion of the pygostyle with the last free caudal as well as the fusion of the post-ilia with the most anterior free caudal does not take place until the bird is nearly adult.

MUSCULATURE

In as much as the woodpecker puts its tail to a greater variety of uses than does most any other bird, the component parts are stronger and better developed. The feathers are stiff and serve well as a prop to support the body while climbing tree trunks. Along with the strong feathers there is a corresponding development in the muscles, especially the depressors of the tail. Six pairs of caudal muscles are present, they will be treated only briefly here.

1. levator coccygeus: this muscle has its origin along the dorso-mesial part of the sacrum and is inserted along the neural spines of the tail. It elevates the tail.
2. lateralis quartus: running along with the levator coccygeus and ventro-laterad to it is this muscle with its origin on the posterior part of the ilium and its insertion laterad to the outermost tail feathers. The function of this muscle is to spread the tail feathers.
3. cruro-coccygeus: the origin of this muscle is on the ventro-posterior part of the ilium, it is inserted on the ventro-lateral portion of the pygostyle and is one of the depressor muscles.
4. depressor-coccygeus: this is a long well developed muscle and serves as the main depressor of the tail. It originates on the femur, passes back through the

other muscles and is inserted on the ventro-lateral part of the pygostyle. It is so arranged that when the femur is thrown forward, as it is when the bird alights on a tree, this muscle is pulled forward and the tail is drawn ventrad against the tree trunk.

5. ischio-coccygeus: this is a wide flat muscle with its origin on the ischium and its insertion laterad to the pygostyle. Its function is to help move the tail ventrally and laterally.

6. pubo-coccygeus: this muscle is similar to the ischio-coccygeus and runs along with it for most of the way. It has its origin on the pubis and is inserted laterad to the tail feathers. It aids inspreading and bringing the tail feathers ventrad.

THE SKELETON

The greater use of the feathers and the development of the muscles calls for a stronger support, so in this family we find highly specialized bones in the tail region. The free caudals are relatively simple, but they have well developed transverse processes, neural spines and chevron bones to serve as levers for the strong muscles. The centra are also large. The greatest development is found in the pygostyle. The neural spine is well developed, a character which is also found in some other birds, but the well developed terminal disc on the ventral aspect is a Picine characteristic and nowhere else is it developed to the extent that it is in the woodpeckers.

In the discussion to follow a detailed description will be given of the caudal vertebrae in the Northern Flicker (*Colaptes auratus luteus*); then the other species will be taken up in their proper order and the similarities and dissimilarities will be noted as they occur. Special attention will be given to the pygostyle as it is the most variable of the bones of the tail.

Colaptes auratus luteus Bangs.-Northern Flicker. In this species as will be seen in some others later, the number of free caudals is variable; depending upon the age of the specimen. As was stated before, in older specimens where fusion of the separate elements is more complete, the number of free movable vertebrae is less than in younger specimens where fusion has not been carried so far. In five specimens examined six free caudals and a pygostyle are in evidence- while in fifteen specimens there are only five free caudals. Each caudal bears on its dorsal surface the prominent neural spine which is roughly cone-shaped and projects anterodorsad from the neural arch. A very small neural canal, almost capillary in some specimens, pierces the neural arch. As one passes forward in the series, the neural spines become shorter and more blunt; in a few of the specimens the anterior two spines show signs of bifurcation.

Very broad and somewhat ventrally inclined transverse processes characterize the five or six free caudals; those of the most anterior pair are usually wider and more compressed dorso-ventrally than those farther caudad; the ends are noticably wider and curve gracefully backwards whereas the posterior ones are curved slightly forward and the middle pair extends almost directly laterad. All but the first pair taper toward the ends. The transverse processes are practically the same length all through the series. The width varies only slightly in different specimens. Chevron bones are to be found on the posterior four segments; they are fused with the centra. The last two of these are bifid and the last one is usually pierced by a foramen which passes through the lower margin of the pygostyle. The centra are large and non-pneumatic.

Consideration will now be given to the peculiarly shaped pygostyle which terminates the series and is so characteristic of the group. This segment varies slightly in different specimens. A typical bone is shown in Plate I fig. 2. The neural spine is tall, being thin-edged in front and on top while posteriorly it is much thicker. The capillary-like neural canal penetrates the pygostyle for a short distance. Posteriorly the pygostyle at its ventral margin flares out as a broad hexagonal plate, the terminal disc, which is a Picine characteristic. At the lower edge of the pygostyle there is a small foramen which, as stated previously, is continuous with that of the ultimate chevron bone. In young specimens this foramen is open at the lower margin, being closed in only on the sides and above by bone (Plate I, fig.10). The lower edges later fuse to form a complete circle. In K.U.Mus.No. 15247 the lower margin is bridged by a very thin bar of bone connecting the two lower points; in the same specimen a transverse foramen passes through the pygostyle just below the transverse processes. In K.U. Mus.No. 15137 the submarginal foramen is very small and instead of appearing at the lower margin as it does in the other specimens it is well up, nearly in the center of the terminal disc. The wide flattened transverse processes are directed forward and ventrad at an angle of about 45 degrees; they taper towards the end, in some of the specimens forming an acute point, while in others this is more blunt and rounded.

Colaptes auratus auratus (Linnaeus) - Flicker. One specimen, U.S.Mus.No. 17915 was classified only to the species; as nearly as could be determined from the skeleton it is a true *auratus*. Two other specimens classified the same way proved to be *Colaptes auratus luteus*. In the one specimen of *Colaptes auratus auratus* there are six free caudals. The transverse processes do not differ from the former species. Three chevron bones, the last two of which are pierced by a foramen, are present on the ventral surface. There is a very prominent submarginal foramen (Plate I, fig.1).

Colaptes chrysoides mearnsi Ridgway.- Mearns's Gilded Flicker.

Here we find a close resemblanse to *Colaptes auratus luteus* in the well defined angles of the pygostyle, the posterior portion of which is deeply concave. However, the width across the transverse processes of the pygo-style, from tip to tip, is proportionally greater than in the former species (Plate I, fig. 3). The transverse processes of the five free caudals are not pointed at the distal end as in *Colaptes auratus luteus*, but are as broad there as they are at the base. The most caudad of the three chevron bones is pierced by a canal that passes back through the ventral margin of the pygostyle.

<u>Colaptes cafer cafer</u> (Gmelin).- Mekican Red-shafted Flicker.

No specimens of this species w ere available for examination. The following information concerning them is given by Dr. R.W. Shufeldt (<u>On the Osteology of the Woodpeckers</u>. Proc. of the Amer. Phil Soc. 1900, vol. 39, pp. 601-604). "Excluding the pygostyle, six free vertebrae compose the skeleton of the tail...The neural canal is almost capillary in its calibre, while in the two ultimate segments a coossified, strong chevron bone, is seen, which is likewise pierced antero-posteriorly in the last one by a foramen. This foramen is also carried on through the lower part of the peculiarly formed pygostyle. The neural spine of the last mentioned is lofty, being thin edged in front and on top, while posteriorly it is thicker. This bone also coossifies with the caudal vertebra next in front of it, the transverse processes of which remain undiminished in size. Behind, the pygostyle at its lower edge flares out as a broad, transversely disposed hexagonal plate of bone, constituting a well known character of the Pici".

<u>Colaptes cafer collaris</u> (Vigors). Red-shafted Flicker. Here the broad transverse processes of the free caudals, as in <u>Colaptes chrysoides mearnsi</u>, show a slight variation

from the somewhat pointed processes in Colaptes auratus luteus. The broadened posterior part o f the pygostyle is somewhat rounded, the angles being less well defined than in the former species (Plate I, fig. 4). There is no canal passing through the last chevron bone as was the case in the other species of Colaptes. In the pygostyle the submarginal foramen is small, being almost capillary in calibre.

Melanerpes erythrocephalus (Linnaeus).- Red-headed Woodpecker.

In six specimens examined there were five free caudals while in two immature specimens six free vertebrae were present. Dr. R.W. Shufeldt in his paper previously mentioned (page 605) states that he finds six free caudals in this species. He possibly examined an immature specimen as five was the number in all adults examined. The transverse processes of these free caudals are similar to those of Colaptes auratus luteus in general shape, but are much smaller. The four chevron bones which are found ossified to their centra are bifid, but the last one is not perforated by a canal as it is in most of Colaptes. The pygostyle is relatively smaller than in Colaptes. The posterior portion is deeply cupped and the edges are rolled over (Plate I, fig. 5b), a character not seen before. A large foramen median in position perforates the lower edge of the pygostyle. In two immature specimens at hand the lower margin of the foramen is not closed, thus leaving a notch in the lower portion. The neural canal is proportionally larger than in Colaptes and extends into the pygostyle for some distance. In one specimen, K.U.Mus.No. 14555, the fusion of the pygostyle with the last free caudal is clearly shown; a small foramen passes through the base of each transverse process dorso-ventrally and the suture not yet fully ossified is still well defined (Plate I,fig. 7).

Centurus carolinus (Linnaeus).- Red-bellied Woodpecker.

Of twelve specimens examined eleven have six free caudals and one, K.U.Mus.No. 13940, has but five. The neural spines are pointed and directed well forward. Four chevron bones are present, the ultimate one may or may not contain a canal that continues through the pygostyle. In the immature specimens the submarginal foramen is not yet closed as was the case in Melanerpes and Colaptes above (Plate I,fig. 10) , described on page 11. The neural spine of the pygostyle is relatively heavier and shorter than in Melanerpes; it is as heavy as the neural spine in Colaptes where the pygostyle is much larger in every other respect. The terminal disc comes to a point at the ventral surface and is more angular than is the former species (Plate I, fig. 6).

Centurus aurifrons (Wagler).- Golden-fronted Woodpecker.

In this species there are six free caudals, the most anterior one is partly fused with the sacrum. The transverse processes of the free caudals are flattened and pointed at the ends, and are not as broad as those in the species above. Four bifid chevron bones are present, there is no foramen. The slightly smaller pygostyle is very similar in every respect to that of *Melanerpes*. The submarginal foramen is pronounced and located near the lower margin of the bone. The neural spine is proportionally thinner and longer than in *Centurus carolinus* (Plate I, fig. 8).

Centurus uropygialis uropygialis Baird.-Gila Woodpecker.

Seven free caudals, the last one nearly fused with the pygostyle, are in evidence. The transverse processes are narrow, flattened dorso-ventrally, and taper to a point at the distal end. The lateral margin of the broad posterior part of the pygostyle is straighter and less convex than in *Centurus aurifrons* (Plate I, fig. 8). There is a prominent submarginal foramen. The chevron bones are three in number and bifid.

<u>Balanosphyra formicivora formicivora</u> (Swainson).

Ant-eating Woodpecker.

Similar to <u>Melanerpes</u>; the one specimen before me has six free caudals, as do the other species of <u>Balanosphyra</u>. The transverse processes are curved ventro-anteriorly. There are four chevron bones. The pygostyle is slightly more deeply cupped and the neutal spine projects farther dorsad than in <u>Melanerpes</u> (Plate I, fig. 11).

<u>Balanosphyra formicivora aculeata</u> (Mearns).-

Mearns' Woodpecker.

In this form the transverse processes are somewhat narrower than in the former species; they come to a dull point on the end. There is no noticable change in the neural spines. Three coössified chevron bones are present. The pygostyle is smaller; a prominent foramen passes through the ventral margin. It is rounded ventrally and not angular as in the former species (Plate I,fig. 12).

<u>Balanosphyra formicivora bairdi</u> (Ridgway).-

California Woodpecker.

The pygostyle differs somewhat in outline from that of the former species. The posterior portion is angular, whereas in the others it is more rounded. It is also slightly larger. Four chevron bones are present, the last one is pierced antero-posteriorly by a canal, a character not present in the other species of Balanosphyra.

Asyndesmus lewisi Riley.- Lewis' Woodpecker. In this form there are six free caudals, the first one being partly fused with the post-ilia. The transverse processes taper toward the distal end. The pygostyle is similar to Melanerpes, but considerably larger with the edges of the posterior terminal disc flattened and not rolled over as was the case in the former species. There is a prominent submarginal foramen(Plate II, fig. 13).

Phloeotomus pileatus pileatus (Linnaeus).- Pileated Woodpecker.
Five skeletons of this genus from the U.S. Natl. Museum were classified only to the species. Two of them proved to be true pileatus and the other three Phloeotomus pileatus abieticola. All of the specimens have six free caudals and a huge pygostyle. The broad flattened transverse processes dip ventrally less than do those of Colaptes. The neural spines are prominent and directed dorso-anteriorly. A large neural canal passes back into the pygostyle for some distance. Three chevron bones, one less than in Colaptes are to be found on the three ultimate vertebrae; the last one is pierced by a foramen which passes on back through the lower edge of the pygostyle. In this respect it resembles Colaptes auratus luteus except for its much greater size (Plate II,fig.15).

There are usually two smaller foramina just above the larger submarginal foramen, and two prominent transverse foramina pass through just beneath the transverse processes. The anterior portion of the neural spine is roughly stair-step in outline.

Phloeotomus pileatus abieticola (Bangs).- Northern Pileated Woodpecker.

This is the largest species as yet considered and differs from the former species in this respect as well as the general shape of the pygostyle (Plate II, fig. 14).

Campephilus imperialis (Gould).- Imperial Woodpecker

Skeletons of this genus were not available for study. However Dr. R.W. Shufeldt (On The Osteology of The Woodpeckers. Proc. of The Amer. Phil. Soc. 1900, vol.39,p605) states that a canal is found through the chevron bones of the caudal vertebrae and that a very high state of pneumaticity exists throughout. As for the number and character of the free vertebrae the writer knows nothing due to lack of material.

Dryobates villosus villosus (Linnaeus).-Hairy Woodpecker.

In all the specimens of this species examined there are six free caudals. The transverse processes are expanded toward the distal end instead of tapering as in Colaptes auratus luteus, And the cetral ones are shorter than those anterior or posterior to them. The neural spines project well forward, the neural canal is small. Three bifid chevron bones are present. From the anterior aspect the pygostyle differs somewhat from the forgoing species in that the lower margin extends farther ventrad from the centrum. Posteriorly, the terminal disc is longer and less pointed at the ventral margin (Plate II fig.16). As to the submarginal foramen Dr. R.W. Shufeldt, in his paper mentioned previously, page 605, makes the following statement; "There is no canal passing through the chevron bones and the lower part of the pygostyle in the skeleton of the tail in Dryobates". No canal was found passing through the chevron bones, but in nearly every case a prominent foramen pierces the lower part of the pygostyle. In one specimen, K.U.Mus.No. 14554, the canal is absent, but it is present in the other twelve examined.

Dryobates villosus audubonii (Swainson).- Southern Hairy Woodpecker.

The transverse processes of the free caudals are narrower and less flattened than those of the preceeding species. The neural spines are more elevated and the capillary neural canal pierces the pygostyle. There are four chevron bones in the specimen before me. The pygostyle is quite different than that of Dryobates villosus villosus; the neural spine projects farther dorsad, the terminal disc is proportionally broader and shorter(PlateII,fig.17).

Dryobates villosus orius Oberholser.- Sierra Woodpecker.

The transverse processes of the six free caudals are flattened dorso-ventrally and bluntly rounded on the distal ends. There are three bifid chevron bones on the three ultimate segments. The pygostyle is slightly larger than that of _Dryobates villosus villosus_, but the width across the transverse processes is lessthan in that species (Plate II, fig. 16).

Dryabates pubescens medianus (Swainson).- Downy Woodpecker.

In this species we find the greatest variation in the number of free caudals. In two specimens examined, K.U.Mus. Nos. 14197 and 14491 there are five free caudals while in K.U.Mus. No. 14173 there are seven. Twenty two other specimens examined have six free tail vertebrae, the usual number found in _Dryobates_. This is one of the smaller forms, the only one smaller that is described here is _Dryobates pubescens turati_, it will be discussed next. The transverse processes of _Dryobates pubescens medianus_ are broader at the base and taper towards the ends; the neural spines are pointed and bent well forward. A capillary canal extends into the pygostyle. The posterior portion of the pygostyle varies slightly in shape in different specimens. The terminal disc usually comes to a point at the ventral margin, or in some cases is more or less rounded (Plate II,fig.19). Of twenty five specimens examined a submarginal foramen was present in nine. Four chevron bones were present on six of them,the other nineteen having but three., The chevron bones are bifid.

<u>Dryobates</u> <u>pubescens</u> <u>turati</u> (Malherbe).- Willow Woodpecker.

In the one specimen before me there are seven free caudals, the ultimate one being nearly fused with the pygostyle. Two prominent chevron bones and anterior to these three smaller ones are present. The pygostyle is the smallest of any species examined; it has a prominent submarginal foramen and is much the same shape as in <u>Dryobates</u> <u>pubescens</u> <u>medianus</u> (Plate II,fig. 20). There is no noticable difference in the transverse processes.

<u>Dryobates</u> <u>nuttallii</u> (Gambel).- Nuttall's Woodpecker. This species is slightly larger than the two preceeding. Six free caudals and a pygostyle make up the framework of the tail. The transverse processes are, as in <u>Dryobates</u> <u>pubescens</u> <u>medianus</u>, broader at the base and taper towards the ends. Four chevron bones are present. A neural canal, so small that it can hardly be discerned with the naked eye, passes through the neural arch into the pygostyle. The terminal disc of the pygostyle tapers towards the lower margin and a tiny canal is present, the neural spine is short (Plate III, fig. 21).

<u>Dryobates</u> <u>scalaris</u> <u>bairdi</u> (Malherbe).- Baird's Woodpecker.

As is typical of most of the <u>Dryobates</u> we find in this species six free caudals and a pygostyle. The transverse processes are very similar to those of the preceeding species. There are four chevron bones. The pygostyle differs from that of <u>Dryobates</u> <u>nuttallii</u> in that the terminal disc is more angular, the neural spine projects proportionally farther dorsad and the submarginal foramen is much more prominent (Plate III, fig. 22).

<u>Dryobates</u> <u>arizonae</u> <u>arizonae</u> (Hargitt).- Arizona Woodpecker.

The usual number of six free caudals are present, however there is a variation in the transverse processes. Instead of tapering toward the ends the processes are somewhat constricted near the base and grow wider distally. Four chevron bones are present, the most anterior one being very small.The terminal disc of the pygostyle is very similar to <u>Dryobates</u> <u>villosus</u> <u>villosus</u> in outline (Plate III, fig. 23), When viewed from the side, the neural spine does not extend as far posteriorly as it does in <u>D</u>.<u>v</u>. <u>villosus</u>.

<u>Xenopicus</u> <u>albolarvatus</u> <u>albolarvatus</u> (Cassin).- White-headed Woodpecker.

In this form there are only five free caudals, the transverse processes of which are broad, short and flat.

The pygostyle is very much like _Dryobates villosus villosus_ in size and shape, but is less deeply cupped on the posterior surface of the terminal disc. A prominent submarginal foramen is present(Plate III,fig.24).

Phrenopicus borealis (Vieillot).- Red-cockaded Woodpecker.

The transverse processes of the six free caudals are narrow and taper slightly toward the ends. There are three chevron bones which are bifid. The pygostyle is similar to that of _Balanosphyra formicivora aculeata_ except that it is somewhat narrower in proportion to its length. A prominent submarginal foramen is present (Plate III,fig.25).

Sphyrapicus varius varius (Linnaeus).-Sapsucker.

In this genus there is the regular number of six free caudals. The slender transverse processes are well apart and taper toward the ends. The neural spines are wide and blunt; all but the posterior one show signs of bifurcation. Four prominent chevron bones are present. The pygostyle is very similar in shape to that of _Melanerpes_, but the transverse processes are not so prominent. The posterior surface of the terminal disc is deeply concave with the edges more or less rolled over as in _Melanerpes_. A large fenestra is present at the lower margin (Plate III fig. 26).

Sphyrapicus ruber ruber (Gmelin).-Red-breasted Sapsucker.

Similar to the above species in every respect except in the pygostyle which is slightly larger; the neural spine is more pointed and the terminal disc is more angular (Plate III,fig.27).

Sphyrapicus thyroideus (Cassin).- Williamson's Waodpecker.

In the one specimen before me, the only variation discernable from the two above mentioned species is in the pygostyle, which is less deeply cupped on the posterior of the terminal disc and has the submarginal foramen higher up from the lower margin. It is more nearly like *Sphyrapicus ruber ruber* than *Sphyrapicus varius varius* (Plate III,fig.28).

Picoides arcticus (Swainson).- Black-backed Three-toed Woodpecker.

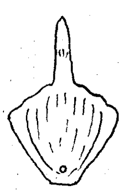
The transverse processes are flattened and expanded at the ends as in *Dryobates villosus villosus*. Three bifid chevron bones are present. In the pygostyle there is a radical change from all the above mentioned species.The neural spine projects but a short distance dorsad to the terminal disc. As viewed from the posterior, the terminal disc differs markedly in outline from the other species; it is roughly four sided, tapers very little towards the lower margin, the corners are rounded and the whole structure is but slightly concave (Plate III,fig.29), whereas in <u>Colaptes</u> and others this structure is angular, tapers to a point at the lower margin, and the neural spine projects well up from the base of the terminal disc. It differs somewhat from the anterior aspect also in that the centrum is farther up from the lower margin. A submarginal foramen, almost capillary in size, is located well up near the center of the terminal disc.

<u>Picoides americanus fasciatus</u> Baird.- Alaskan Three-toed Woodpecker.

Similar to <u>Picoides arcticus</u> but smaller. The pygostyle is likewise more angular similating somewhat that of <u>Dryobates villosus villosus</u> but much broader at the base (Plate III, fig.30).

COMPARISON WITH OTHER SPECIES

It is interesting to compare the pygostyle of the woodpecker with that of the White-breasted Nuthatch (*Sitta carolinensis carolinensis* Latham.) and the Brown Creeper (*Certhia familiaris americana* (Bonaparte), both of which use their tails to some extent in climbing about the tree trunks, but less extensively than the woodpecker. The following drawings show the comparative development in the three forms, namely, *Dryobates pubescens medianus*, *Certhia familiaris americana* and *Sitta carolinensis carolinensis*; Nos. 1,2,and 3 respectively. The drawings are twice natural size. These three species are all about the same size, the Brown Creeper being the smallest, but having the tail feathers developed better than the Nuthatch although not as well as the Downy Woodpecker (*Dryobates pubescens medianus*).



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It is evident from the above drawings that the bird which uses its tail in the greatest variety of ways and the most extensively has the best developed pygostyle. It is best developed in the Downy Woodpecker, less in the Brown Creeper and still less in the White-breasted Nuthatch.

EXPLANATION OF TABLES

Measurements of the pygostyle and the skull are given in millimeters in the following tables. In table I each specimen is listed with its respective measurements and the percentage of pygostyle as compared with the skull is given in a seperate column under that head. In each species the group in which the greatest number of individuals fell is designated as the mode. The mode of each species, the maximum and minimum percentage, and the number of specimens measured is given in table II.

It will be seen that in such genera as Colaptes, Melanerpes, Centurus, Balanosphyra, and Asyndesmus , where much of the food is secured from the ground, in the air or without much pecking, and the frontals of the skull do not roll over the pre-maxillaries at the cranio-facial hinges (a character assigned to those that do the most pecking), the percentage of pygostyle does not exceed 30%. In the other genera, Phloeotomus being the only one where the frontals do not roll over the premaxillaries at the cranio-facial hinge, the percentage is 30% or above, being the highest in the species Sphyrapicus thyroideus at 39.2%. There seems to be a direct correlation between the size of the pygostyle and the extent to which the bird uses its tail in climbing or in clinging to the trunk of trees.

TABLE I

Species	Number	Sex	LP	WP	PS	TrP	LS	%
Colaptes a. auratus	US17915	M	16.9	10.8	7	11.8	60.2	28.2
Colaptes a. luteus	KU13406	M	16.8	11.7	8	12.9	57.9	29.1
'' '' ''	KU11339	M	17.5	12.1	7.9	13.7	61.5	28.4
'' '' ''	KU15761	M	17.9	11.7	8.6	13.1	59.0	30.3
'' '' ''	KU14509	M	14.5	8.3	7.5	10.0	56.1	25.9
'' '' ''	KU15420	M	16.6	10.7	8.7	12.5	59.7	27.8
'' '' ''	KU14597	M	16.3	11.2	8.3	11.8	57.0	28.6
'' '' ''	KU15773	M	16.9	11.3	8.8	12.5	58.1	29.0
'' '' ''	KU13407	M	17.3	----	8.8	11.6	61.0	28.6
'' '' ''	KU15247	M	17.1	11.1	8.1	12.2	59.0	29.0
'' '' ''	US16692	M	16.0	10.1	6.6	10.8	57.4	28.0
'' '' ''	US224489	M	16.0	11.0	8.0	12.0	58.8	27.3
'' '' ''	KU13569	F	15.3	11.0	7.0	10.6	58.5	26.2
'' '' ''	KU13363	F	15.7	10.7	7.2	11.2	55.2	28.5
'' '' ''	KU13408	F	17.1	11.2	8.4	11.4	58.7	29.1
'' '' ''	KU14159	F	16.0	10.3	8.0	10.0	55.7	28.7
'' '' ''	KU15231	F	16.3	12.2	7.0	12.0	56.4	28.9
'' '' ''	KU15951	F	17.3	10.4	9.0	13.0	60.3	28.7
'' '' ''	KU14332	F	17.3	11.8	7.8	13.4	59.0	29.3
'' '' ''	KU15137	F	17.3	12.3	9.3	----	59.0	29.3
'' '' ''	KU15025	F	16.8	10.7	8.0	11.9	58.8	28.5
'' '' ''	KU14019	F	16.7	12.0	7.4	12.2	58.5	28.5
Colaptes c.mearnsi	US225779	M	17.0	10.9	7.4	13.4	60.8	27.9
Colaptes c.collaris	KU14610	M	17.0	11.9	8.1	11.5	61.0	27.9
Melanerpes erythrocephalus	KU14329	M	13.6	8.5	7.6	8.0	49.7	27.3
'' ''	KU13561	M	14.3	8.0	7.1	----	49.9	28.6
'' ''	KU15768	M	12.9	8.4	7.0	8.6	47.5	27.2
'' ''	KU15741	M	12.3	8.4	6.7	9.2	48.0	25.6
'' ''	KU15665	M	12.1	8.0	6.4	8.5	48.7	24.8
'' ''	KU15707	M	13.0	8.3	6.9	8.6	50.9	25.6
'' ''	KU14555	M	14.1	8.7	7.0	10.0	49.0	28.8
'' ''	KU15024	M	11.0	7.6	~~7.5~~	7.5	44.3	25.0
'' ''	KU14500	M	13.7	8.3	7.1	9.0	48.8	28.1
'' ''	KU13460	F	12.6	9.0	6.7	8.1	45.7	27.5
'' ''	KU15700	F	12.6	8.3	7.0	7.9	47.0	26.8
'' ''	KU14503	F	13.2	8.6	6.5	9.1	47.4	27.8
'' ''	KU15728	F	12.7	8.0	6.8	8.3	47.0	27.0
Centurus carolinus	KU13425	M	14.0	8.5	6.7	8.5	51.6	27.1
'' ''	KU14034	M	14.9	9.4	6.7	10.1	53.9	27.6
'' ''	KU14206	M	15.5	9.8	7.5	9.7	53.4	29.0
'' ''	KU14957	M	14.8	9.7	7.6	9.1	51.9	28.6
'' ''	KU13990	M	14.5	9.2	7.7	8.4	54.0	27.8

TABLE I (cont)

Species	Number	Sex	LP	WP	PS	TrP	LS	%
Centurus carolinus	KU13940	M	14.2	9.4	6.0	9.6	50.8	27.9
'' ''	KU13141	?	14.6	8.o	7.1	---	51.9	28.1
'' ''	KU14495	~~?~~	14.3	8.8	7.1	9.2	50.8	28.1
'' ''	KU15592	?	14.5	10.0	7.7	9.5	56.0	25.9
'' ''	KU15416	F	14.3	9.2	7.2	9.1	50.5	28.3
'' ''	KU12525	F	14.0	8.7	6.9	8.0	49.3	28.4
Centurus aurifrons	KU15171	?	14.6	9.1	7.2	8.5	52.0	28.1
'' ''	KU15280	F	14.6	9.3	7.6	9.1	51.5	28.3
'' ''	KU15170	F	14.5	8.8	6.7	9.6	50.8	28.5
Centurus uropygialis	US224112	M	14.0	9.8	6.8	9.3	52.4	26.7
Balanosphyra f. formicivora	US288806	?	14.2	---	6.9	---	47.5	30.0
B. f. aculeata	US225777	M	13.5	8.1	6.9	8.9	47.0	28.7
'' '' '' ''	US225775	F	13.7	7.9	6.5	8.1	44.4	30.9
Asyndesmus lewisi	KU14615	M	16.7	9.9	8.7	11.0	55.5	30.1
Phloeotomus p. pileatus	US19346	?	24.1	15.4	11	16.0	72.1	33.4
P. p. abieticola	US 224465	M	27.5	17.6	11	19.4	85.8	32.1
'' '' ''	US17867	?	26.0	16.5	11.8	17.9	82.6	31.5
'' '' ''	US17869	?	27.0	17.5	12	19.0	79.1	34.0
Dryobates v.villosus	KU15591	M	16.1	10.3	7.0	9.5	47.7	33.6
'' '' ''	KU15519	M	15.9	10.2	7.3	10.9	49.0	32.5
'' '' ''	KU14507	M	15.7	9.9	7.0	10.1	45.6	34.6
'' '' ''	KU15114	M	16.0	9.4	7.5	----	45.0	35.5
'' '' ''	KU15169	M	15.1	10.0	6.6	9.7	47.7	31.6
'' '' ''	KU11681	F	14.6	9.1	6.6	9.0	45.0	32.4
'' '' ''	KU15781	F	15.2	9.8	6.7	9.5	47.7	31.8
'' '' ''	KU14554	F	14.6	10.0	6.2	9.1	44.7	32.6
'' '' ''	KU15159	F	15.5	9.4	7.1	8.9	46.5	33.4
'' '' ''	KU14782	F	15.0	9.1	6.6	9.7	48.1	31.1
D. v. audubonii	US226437	F	13.7	9.0	6.8	----	43.1	31.8
D. v. orius	--------	M	16.0	10.4	6.9	9.2	48.0	33.3
D. pubescens medianus	KU15003	M	10.7	6.8	4.8	6.9	32.5	32.9
'' '' ''	KU14173	M	10.1	7.0	4.5	6.1	30.7	32.1

TABLE I (cont)

Species	Number	Sex	LP	WP	PS	TrP	LS	%
D. p. medianus	KU14198	M	11.3	7.3	5.0	7.1	32.6	34.7
" " "	KU14035	M	10.5	6.9	5.0	6.9	31.0	33.8
" " "	KU14496	M	10.6	6.9	4.8	6.9	32.0	33.1
" " "	KU13948	M	10.4	7.0	4.7	6.6	31.3	33.2
" " "	KU15418	M	11.2	6.7	5.7	6.9	33.2	33.7
" " "	KU15035	M	10.8	6.8	5.0	6.5	32.0	33.7
" " "	KU11267	M	11.3	6.9	5.4	7.1	31.7	35.6
" " "	KU15482	M	10.7	7.3	5.1	7.0	31.7	33.7
" " "	KU12815	?	10.5	6.8	5.0	6.7	31.5	33.3
" " "	KU13951	F	10.2	6.5	4.5	6.1	31.5	32.3
" " "	KU13121	F	9.5	6.3	4.0	5.9	30.6	31.0
" " "	KU13461	F	10.6	6.3	4.6	6.2	30.7	34.5
" " "	KU14169	F	10.7	7.1	5.1	6.8	31.0	34.4
" " "	KU14036	F	9.7	6.8	4.4	6.1	30.2	32.3
" " "	KU13991	F	11.0	7.7	5.0	6.9	31.6	34.8
" " "	KU13104	F	11.2	7.7	5.1	---	30.0	37.6
" " "	KU15679	F	10.6	7.0	5.1	6.7	31.0	34.2
" " "	KU14037	F	10.7	7.1	5.0	6.7	31.3	34.2
" " "	KU14497	F	11.0	7.1	5.2	7.0	31.4	35.0
" " "	KU15417	F	10.5	6.8	4.8	6.0	32.0	32.8
" " "	KU14499	F	10.2	6.7	4.9	6.1	31.7	32.1
" " "	KU11338	F	11.0	7.4	4.8	7.2	31.7	34.7
" " "	KU12816	F	11.0	6.8	5.4	6.5	31.6	34.8
D. p. turati	US226373	M	10.3	6.6	5.1	6.5	31.7	32.5
D. nuttallii	US226371	F	11.6	7.8	4.7	7.8	36.7	31.6
" "	US226372	M	11.2	7.4	4.5	7.8	36.7	30.5
D. scalaris bairdi	US224114	M	11.0	6.8	5.3	7.3	37.5	29.3
" " "	US224115	M	11.1	7.8	5.4	6.8	36.3	30.8
" " "	KU15273	F	11.0	7.3	5.3	7.7	34.2	32.2
D. a. arizonae	US224113	M	13.5	8.4	5.8	8.1	41.8	32.2
Xenopicus a. albolarvatus	MVZ30889	M	15.0	9.4	6.8	9.6	44.1	34.0
Phrenopicus borealis	US224107	M	13.5	8.7	5.8	---	37.8	35.6
Sphyrapicus v. varius	KU15279	F	13.9	8.2	7.3	8.2	36.8	37.8
S. r. ruber	US226370	F	14.0	8.7	6.8	8.1	36.2	38.7
S. thyroideus	US226369	M	13.7	9.3	6.4	8.5	35.0	39.2
Picoides arcticus	US288095	F	16.0	11.8	6.3	---	49.8	32.1
P. a. fasciatus	US288096	F	13.0	9.0	5.2	9.1	40.8	31.8

TABLE II

Species	No.Ex.	Max.%	Min.%	Mode
Colaptes a. auratus	1	28.2	28.2	28.2
C.a. luteus	21	30.3	25.9	28.5
C. c. mearnsi	1	27.9	27.9	27.9
C. c. collaris	1	27.9	27.9	27.9
Melanerpes erythrocephalus	13	28.8	24.8	27.5
Centurus carolinus	11	29.0	25.9	28.5
C. aurifrons	3	28.5	28.1	28.3
Centurus uropygialis	1	26.7	26.7	26.7
Balanosphyra f. formicivora	1	30.0	30.0	30.0
B. f. aculeata	2	30.9	28.7	29.0
Asyndesmus lewisi	1	30.1	30.1	30.1
Phloeotomus p. pileatus	1	33.4	33.4	33.4
P. p. abieticola	3	34.0	31.5	32.0
Dryobates v. villosus	10	35.5	31.1	32.0
D. v. audubonii	1	31.8	31.8	31.8
D. pubescens medianus	25	37.6	31.0	34.5
D. p. turati	1	32.5	32.5	32.5
D. nuttallii	2	31.6	30.5	31.0
D. scalaris bairdi	3	32.2	29.3	30.0
Dryob. arizonae	1	32.2	32.2	32.2
Xenopicus a. albolarvatus	1	34.0	34.0	34.0
Phrenopicus borealis	1	35.6	35.6	35.6
Sphyrapicus v. varius	1	37.8	37.8	37.8
S. ruber ruber	1	38.7	38.7	38.7
S. thyroideus	1	39.2	39.2	39.2
Picoides arcticus	1	32.1	32.1	32.1
P. americanus fasciatus	1	31.8	31.8	31.8

For explanation of the abbreviations used in the above tables see page 4.

SUMMARY

In modern birds the shortening of the tail is due to the compression and fusion of the seperate bones, and not necessarily to a reduction in their number. The large pygostyle with the lower terminal disc is characteristic of all Picine birds. The centra are large and the transverse processes are prominent. The muscles of the tail are also highly developed. The number of free caudals varies from five to seven in different species. Individuals of the same species often vary as greatly in the number of free caudals. In *Dryobates pubescens medianus* the number varies from five to seven. The older birds have the smaller number since fusion has proceeded farther. Six segments fuse to make up the pygostyle in *Colaptes auratus luteus*.

The transverse processes in most species taper toward the distal end, exceptions to this are: *Dryobates villosus villosus*, *Dryobates arizonae arizonae*, and *Picoides*, where the transverse processes are expanded toward the distal end.

The neural spines often show signs of bifurcation, especially in *Colaptes* and *Sphyrapicus* . The chevron bones are coossified with the centra; in the larger species the posterior one or two of these is usually pierced by an antero-posterior foramen; in the smaller species they are merely bifid. The pygostyles are quite characteristic of the species, they differ markedly in size and shape.

CONCLUSIONS

It seems as though in the tail of the woodpecker we have a splendid example of functional adaptatinn. The greater use of the tail feathers probably brought about a strengthening of the parts. This called for a stronger support so the bones and muscles became stronger to meet the demand of the tail feathers. However, J. Arthur Thompson (Biology of Birds, 1923, p.56) makes the following statement; "It is interesting to find that the ploughshare bone is particularily large in birds with strong tail feathers. This may be well seen in the woodpeckers where the tail feathers serve as a prop in climbing a tree. This illustrates functional adaptation. But it does not follow that the usage of the feathers made the pygostyle large." To me at least,it would appear as though the greater use of the feathers was one of the main causes, if not the primary cause of the enlargement of the pygostyle, otherwise the pygostyle and feathers would have developed independently of each other and along the same line, which is not impossible, but very improbable. The proportionally larger pygostyles in birds that use their tails to a greater extent, namely, feed wholly on the tree trunks as do *Dryobates*, *Sphyrapicus* and *Picoides*, instead of partly on the ground or in the air as *Colaptes* and *Melanerpes*, tends to strengthen the above statement.

When we come to study the form of the pygostyle carefully we are struck by the differences in different species which a casual observer would probably not notice. There is a slight variation in individuals of the same species but the general form is always the same. The differences to be found in the various species are, I believe, sufficiently great to make them of real taxonomic value. However it would probably be very difficult to determine the species by the pygostyle alone although it could possibly be done in some cases such as Phloeotomus, Picoides and several of the species of Dryobates; it would not be difficult to place them in the geneus. When the remainder of the skeleton is present the identification can be certainly made in most forms. Further research is needed along this line either to substantiate or discard many of the subspecies which are distinguished only by a slight variation in color or size.

PLATE I

Fig. 1- Colaptes auratus auratus X2.

A, anterior and B, posterior of pygostyle.

Fig. 2- Colaptes auratus luteus X2.

A, anterior and B, posterior of pygostyle, note wider, more angular outline than Fig. 1 or 3.

Fig. 3- Colaptes chrysoides mearnsi X2.

A, anterior and B, posterior of pygostyle.

Fig. 4- Colaptes cafer collaris X2.

A, anterior and B, posterior of pygostyle, note bulging sides and more rounded appearance, also projecting neural spine.

Fig. 5- Melanerpes erythrocephalus X2.

A, anterior and B, posterior of pygostyle, note long,narrow neural spine and rolling edges in B.

Fig. 6- Centurus carolinus X2.

A, anterior and B, posterior of pygostyle, note heavy spine, also straight lines on sides of terminal disc coming nearly to a point on the ventral margin.

Fig. 7- Melanerpes erythrocephalus X2.

Showing fusion of last free caudal and pygostyle.

Fig. 8- Centurus aurifrons X2.

A, anterior and B, posterior of pygostyle showing long slim spine; base similar to Fig. 5.

Fig. 9- Centurus uropygialis X2.

A, anterior and B, posterior of pygostyle.

Fig. 10- _Colaptes auratus luteus_ X2.

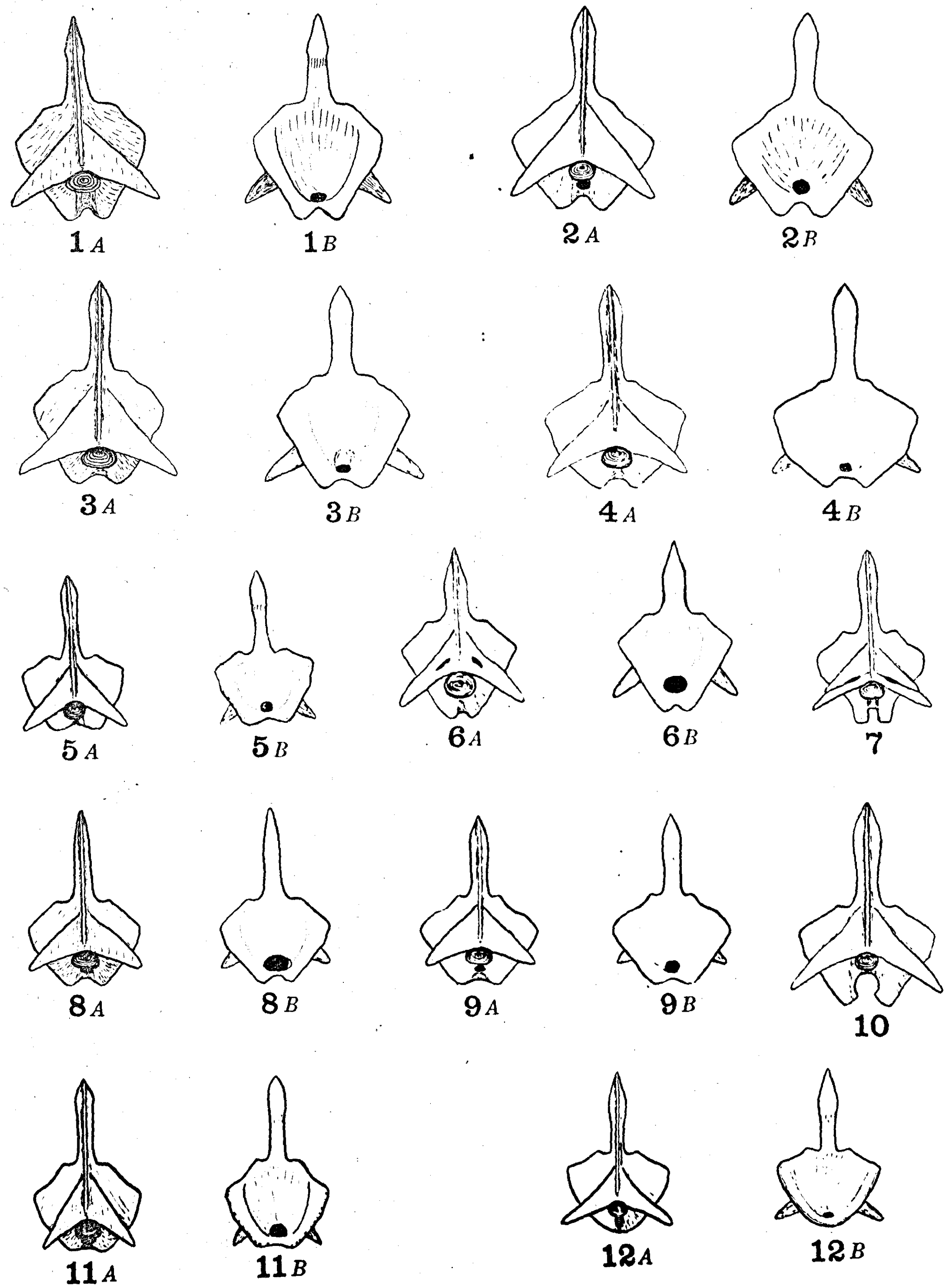
An immature specimen showing the open submarginal foramen at the ventral edge.

Fig. 11- _Balanosphyra formicivora formicivora_ X2.

A, anterior and B, posterior of pygostyle, note the rolled edges of the terminal disc as in Fig. 5B.

Fig. 12- _Balanosphyra formicivora aculeata_ X2.

A, anterior and B, posterior of pygostyle, note the projecting spine and the peculiarly rounded ventral part of the terminal disc.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9B
10
11A
11B
12A
12B

PLATE II

Fig. 13- Asyndesmus lewisi X2.

A, anterior and B, posterior of pygostyle, similar to Fig. 5 but larger.

Fig. 14- Phloeotomus pileatus abieticola X2.

A, anterior and B, posterior of pygostyle. The largest species represented, note the large submarginal foramen and the depression just above where a smaller foramen passes obliquely through.

Fig. 15- Phloeotomus pileatus pileatus X2.

A, anterior and B, posterior of pygostyle. Somewhat smaller than Fig. 14, the angles are more sharply defined and the sides are curved in.

Fig. 16- Dryobates villosus villosus X2.

A, anterior and B, posterior of pygostyle showing relatively short spine and elongated terminal disc, also long transverse processes.

Fig. 17- Dryobates villosus audubonii X2.

A, anterior and B, posterior of pygostyle, smaller than Fig. 16, note the heavy spine.

Fig. 18- Dryobates villosus orius X2.

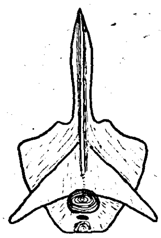
A, anterior and B, posterior of pygostyle, similar to Fig. 16 but the transverse processes spread less, the dides are slightly concave.

Fig. 19- Dryobates pubescens medianus X2.

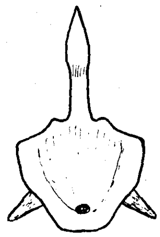
A, anterior and B, posterior of pygostyle, small and angular in outline.

Fig. 20- _Dryobates_ _pubescens_ _turati_ X2.

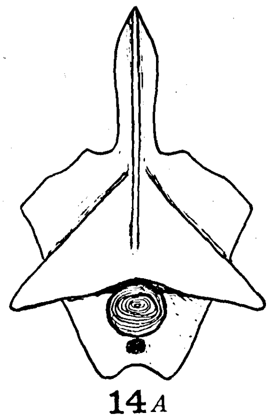
A, anterior and B, posterior of pygostyle, the smallest species represented; note the pointed ventral margin.



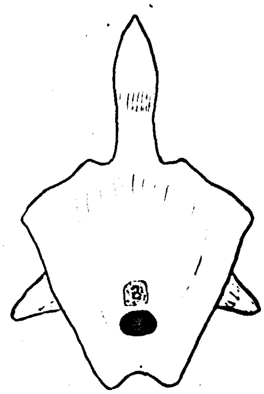
13*A*



13*B*



14*A*



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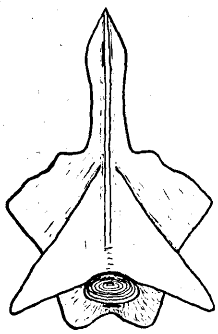
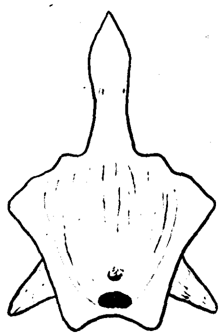
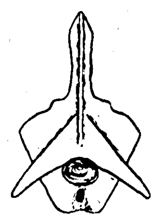


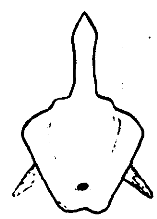
15*A*



15*B*



16*A*



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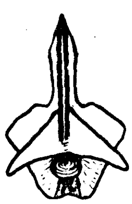

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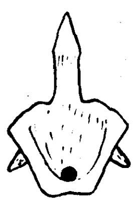

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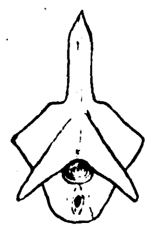

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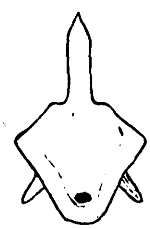

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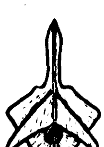

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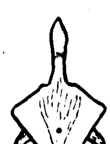

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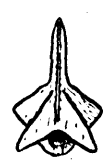

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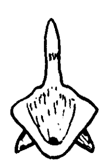


20*B*

PLATE III

Fig. 21- Dryobates nuttallii X2.

A, anterior and B, posterior of pygostyle, note the short spine, rounded terminal disc and heavy transverse processes.

Fig. 22- Dryobates scalaris bairdi X2.

A, anterior and B, posterior of pygostyle, not a typical Dryobates, but more like Melanerpes Fig. 5 .

Fig. 23- Dryobates arizonae arizonae X2.

A, anterior and B, posterior of pygostyle, note the short spine and elongated terminal disc as is typical of the genus.

Fig. 24- Xenopicus albolarvatus albolarvatus X2.

A, anterior and B, posterior of pygostyle.

Fig. 25- Phrenopicus borealis X2.

A, anterior and B, posterior of pygostyle, note the rounded terminal disc as in Fig. 12.

Fig. 26- Sphyrapicus varius varius X2.

A, anterior and B, posterior of pygostyle, note the rolled edges of the terminal disc as in Fig.5.

Fig. 27- Sphyrapicus ruber ruber X2.

A, anterior and B, posterior of pygostyle.

Fig. 28- Sphyrapicus thyroideus X2.

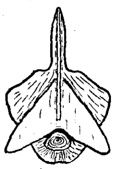
A, anterior and B, posterior of pygostyle.

Fig. 29- _Picoides arcticus_ X2.

A, anterior and B, posterior of pygostyle, note the short heavy spine and the almost rectangular terminal disc with a small submarginal foramen well up from the lower margin.

Fig. 30- _Picoides americanus fasciatus_ X2.

A, anterior and B, posterior of pygostyle, somewhat smaller than Fig 29, but of the same general shape. The submarginal foramen is larger.



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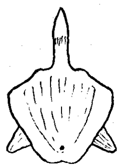

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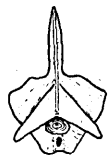

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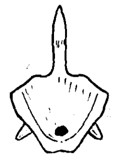

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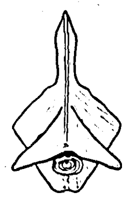

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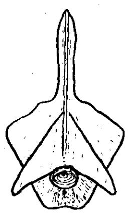

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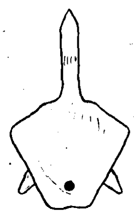

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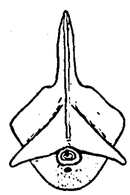

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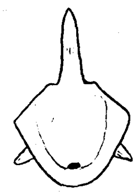

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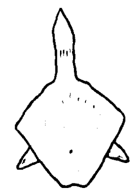

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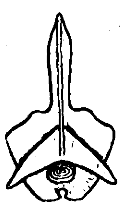

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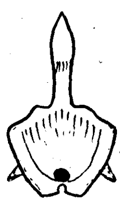

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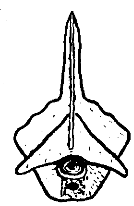

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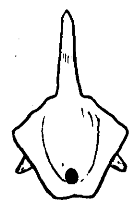

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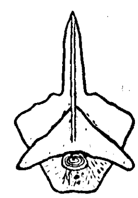
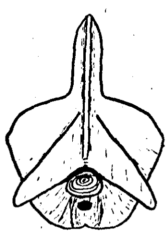


28A



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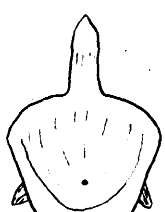

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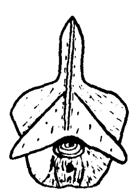

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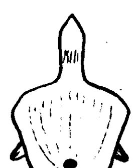

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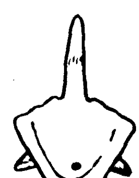

28B

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